XV.

The History of Balanoglossus and Tornaria.

BY ALEXANDER AGASSIZ.

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AMONG the many pelagic invertebrate larvæ discovered by Müller, of which the development remained long unknown, Tornaria is one of the most interesting. Previous to the preliminary notice given by Metschnikoff[1] in 1869, it had been taken for granted that Tornaria was the larva of some genus of star-fish. Discovered by Müller[2] in 1848, Tornaria was subsequently studied by Krohn[3] in 1853. Müller gave a very full account of the younger stages; Krohn's paper, though not adding materially to our knowledge of this larva, complemented the descriptions of Müller in a few particulars. Nothing further was written on the subject till 1866, when I published a short paper on some points of the development of Tornaria[4] which had not been noticed in the young stages described by Müller. This additional information seemed to settle definitely the star-fish nature of the larva, and I accepted unhesitatingly, as well as my predecessors, Müller's views of the affinities of Tornaria. It was only subsequent to the publication of my paper that Dr. Fritz Müller[5] called my attention to a so-called heart, discovered by him in a species of Tornaria from the shores of Desterro. This heart, situated at the base of the canal leading from the water-system to the dorsal pore, is the only organ of Tornaria throwing some doubt on the then generally accepted systematic position of the larva, and I began seriously to doubt the correctness of the homologies I had carried out between the arms of Brachiolaria edged with vibratile cilia and dotted with pigment-cells and the similar ciliated bands of Tornaria.

Müller, Krohn, and myself attached altogether too little value to the large promi-

[1] METSCHNIKOFF, EL. Göttinger Nachrichten, 1869, No. 15, p. 287.

[2] MÜLLER, J. Ueber die Larven u. die Metam. d. Echinod. Abhandl. II., Berlin, 1849; Ueber die Larven u. die Metam. d. Holoth. u. Aster. Abhandl. III., Berlin, 1850.

[3] KROHN, A. Müller's Archiv für Anat. u. Phys., 1853.

[4] AGASSIZ, ALEX. Tornaria, Ann. Lyceum Nat. Hist., VIII., New York, 1866.

[5] MÜLLER, F. In Keferstein's Bericht for 1867.

nent band of vibratile cilia separating the body of Tornaria into two such unequal portions. The presence of a somewhat similar circular band in the larvæ of Holothurians and of Comatulae seemed a powerful argument, in addition to other important structural evidence, in favor of the echinodermoid character of the larva. The analogy between Tornaria and the earlier stages of Brachiolaria is so great that in my paper on the Embryology of the Star-fish I called one of the early stages of Bipinnaria the "Tornaria stage." This striking resemblance is, however, only an analogy, as a memoir published by Metschnikoff in 1870[1] leaves no doubt that Tornaria is the larva of an Annelid and has nothing to do with the Star-fishes.

The exceptionable character of the development of Tornaria made it desirable that the observations of Metschnikoff should be repeated, and the genus of Annelids, of which it is the larva, definitively determined. Metschnikoff threw out the hint that it was, if not Balanoglossus, at least a genus most closely allied to it, — a view which is fully confirmed by the observations I have made of Tornaria, and of a species of Balanoglossus from the coast of New England, connecting the young Annelid raised directly from Tornaria with very small specimens of Balanoglossus found buried in the sand. Metschnikoff certainly showed great sagacity in recognizing as the larva of Balanoglossus the young Annelid he first found pelagic in Naples;[2] but the discrepancy between the two stages then known is so great that his view could hardly be accepted without more tangible proof. The young Annelids which I succeeded in raising directly from Tornaria are considerably older than any observed by Metschnikoff, and they are at the same time but slightly younger than very young specimens of the Balanoglossus found living upon our beaches.

Huxley,[3] in his report upon the researches of Müller, proposed to unite the Echinoderms with the Articulates; but, as he based his opinion entirely upon the figures of Müller, and not upon original investigations, his conclusion, however ingenious and original it may be, and based upon very striking analogical resemblances, is nothing but a hint thrown out for the benefit of investigators. Müller[4] himself regarded the analysis of his paper as most ingenious, but by no means as conclusive; although at that time he had already discovered the peculiar mode of development of some Planarians apparently most closely allied in its general features with the plan of develop-

[1] METSCHNIKOFF, EL. Untersuchungen ueber die Metamorphose einiger Seethiere, Zeitschr. f. Wiss. Zool., 1870, p. 131.

[2] METSCHNIKOFF, EL. Die Larve v. Balanoglossus, Müll. Arch. 1866, p. 592.

[3] HUXLEY, T. H. Report upon the Researches of Müller, Ann. Mag. N. H., VIII., 1851.

[4] MÜLLER, J. Ueber den Allgemeinen Plan in der Entwickelung d. Echinodermen, 1853, p. 19. See also AGASSIZ, ALEX. Embryology of the Starfish, 1864.

ment of Echinoderms. The majority of English naturalists have adopted Huxley's views without further investigation.

Tornaria presents the startling anomaly of an apparently genuine Echinoderm larva, at least till lately so considered by all writers on the subject, developing into an Annelid, and seems at first sight a conclusive proof of the views entertained by Huxley; but, as I think I shall show in the description of the development of Tornaria, the position taken by Huxley is not strengthened, and the gap left between the mode of development of Planarians and other Annelids, as compared with the development of Echinoderms, is as great as ever, in spite of the very striking analogy in the mode of development of some Echinoderms (especially Holothurians and Comatulae) with that of Nemertians, as shown by Müller[1] and Metschnikoff.[2] The history of Tornaria tends, on the contrary, to show a much closer relationship between the Nemertians and the Annelids proper than is generally credited, the development and anatomy of Balanoglossus showing it to be closely allied to Terebellidae, Clymenidae, and allied Annelids, as already suggested by Metschnikoff and Kowalevsky. And, now that we know its ultimate development, the larva presents points of resemblance to well-known Annelid larvæ (Lovén's Larva) which are apparent enough when demonstrated, but so completely hidden by the more prominent pseudo-echinodermal features as readily to have escaped notice.

The presence of the large water-system, riding with its spurs upon the anterior extremity of the alimentary canal, and connecting with the exterior by means of a canal and a dorsal pore, exactly as in the larvæ of the Echinidae, Star-fishes, Ophurians, and other Echinoderms, seems at first sight an overwhelming proof of the position taken by Huxley. But, as I have already shown in my Embryology of the Star-fish,[3] Huxley, misled by the names given by Müller to some of these larvæ ("Wurmförmige Larven"), has revived the old opinion of Oken, and associated the Echinoderms with the Articulates. The hypothetical form to which Huxley reduces these larvæ to make his comparisons and to draw his inferences is one which has never been observed, and as far as we now know does not exist. The larvæ of all the principal types have been described by Müller, Krohn, Thomson, Metschnikoff, and myself. The development of the water-system from the digestive cavity has not been traced in Tornaria; while the lappets of Tornaria, which have nothing to do with the water-

[1] Müller, J. Ueber eine eigenthümliche Wurmlarve ..... Müll. Arch., 1850, p. 485.

[2] Metschnikoff, El. Studien üb. d. Entwickel. der Echinod. u. Nemertinen, Mém. Acad. St. Petersb., 1869, XIV. No. 8.

[3] Agassiz, Alex. Embryology of the Star-fish, 1864, p. 60.

system are developed from the digestive as diverticula. So that the water-system of Tornaria, in spite of its dorsal pore, can in no way be homologized with the water-system of Echinoderms, even if, in addition to the different mode of its development, the presence of a heart and of a muscular band supporting it did not show that we had to deal with an organ which has no homologue in any of the numerous Echinodermoid larvæ thus far observed.

As far as we know the Embryology of the Planarians, of which the development is somewhat analogous to that of Echinoderms, as known from the observations of Müller and Metschnikoff, we still have between the two modes of development radical differences. In all Echinoderms, without exception, the young Echinoderm is developed upon the water-system of the Pluteus as a bud, as it were, and gradually encroaches upon the scaffolding which has supported it, and finally resorbs the whole Pluteus within itself. No such mode of transformation exists in any known Planarian or other Annelid larva. In this group we find without exception that the transformations consist of a very gradual change of one stage into another, and that by an elongation or contraction of the different parts of the larva at its various stages of growth, and by a gradual modification of the topography of the organs, the larva passes little by little into its adult stage, — a condition of things entirely fulfilled by the development of Tornaria into Balanoglossus, which, as far as the last phase of its growth, the Balanoglossus, certainly shows nothing bearing any affinity to the Echinodermoid mode of budding upon the water-system of the Pluteus.

We possess fortunately an admirable anatomy of Balanoglossus by Kowalevsky,[1] who has rediscovered, as it were, the Balanoglossus first figured by Delle Chiaje,[2] and about which nothing of any value, except the short notices of Keferstein[3] and of Quatrefages,[4] had been written since Delle Chiaje's time. I shall therefore, in referring to Kowalevsky's memoir, be able, from the study of the young immediately following the Tornaria stage and of younger specimens of Balanoglossus than those Kowalevsky has investigated, to give an explanation of the nature and function of many of the organs of this interesting animal which could not be explained merely from the study of the adult.

As is well known from Müller's figures and descriptions of the youngest stages of Tornaria, the large circular belt of vibratile cilia is only developed in the older

[1] Kowalevsky. Anatomie du Balanoglossus, Mém. Acad. St. Pet., 1866, X. No. 3.

[2] Delle Chiaje. Mem. sull. Stor. e Not. degl. Anim. s. Verteb., Pl. LVI., f. 36.

[3] Keferstein. Zeitschrift f. Wiss. Zool., 1863, XII. 91.

[4] Quatrefages. Ann. Sc. Nat., 1846, VI. p. 184.

stages; in the youngest specimens observed, the muscular band connecting the extremity of the water-system to the base of the eye-spots is present. These two features are not known in any other Echinoderm larva, and were sufficient to have shown the possibility of Tornaria proving the larva of an Annelid. In the well-known Annelid larva of Lovén[1] (which, according to my observations,[2] develops into a Nemertian, while Schneider[3] thinks it is the larva of Polygordius) we find the same muscular band starting from the base of the eye-specks, and in older stages the circular anal belt of vibratile cilia. Owing, however, to the great number of rings below the anterior part of the larva, and the presence of a prominent anterior ring of vibratile cilia above the mouth, the close resemblance between Lovén's Larva and Tornaria is not so striking at first sight as it really is. In Tornaria the prominent belt of large vibratile cilia appears at a comparatively late period, yet long before any of the rings of the posterior part of Balanoglossus; while in all Annelid larvæ which have a similar anal belt of vibratile cilia this belt is the earliest to make its appearance, long before there is any trace of the formation of the rings of the posterior part of the body. I would refer to the figures of Annelid larvæ given by Milne-Edwards,[4] Sars,[5] Busch,[6] Müller,[7] Claparède,[8] Max Müller,[9] Krohn,[10] Metschnikoff,[11] and myself,[12] for comparison with Tornaria.

The figures of Tornaria given in this paper precede immediately its transformation into young Balanoglossus; for the earlier stages I would refer to the figures given by Müller, Metschnikoff, and myself. The oldest stages of our Tornaria differ materially from those described by Metschnikoff. He speaks of a second smaller anal band of vibratile cilia, between the broad band and the anal opening. I have not found this second band in any specimens of our Tornaria, and in our species this band does not exist. Metschnikoff represents the "Wurstförmige Körper" as appendages of the intestine, and as different from what he has called the lateral plates, or appendages of the

[1] Lovén. Jakttagelse öfser Metamorfos hos en Annelid, K. Vet. Akad. Handl. Stockholm, 1840, p. 93.

[2] Agassiz, Alex. On the Young Stages of a few Annelids, Ann. Lyceum Nat. Hist., New York, 1866, p. 303.

[3] Schneider. Bau u. Entwickelung v. Polygordius, Müll. Arch., 1868, p. 51.

[4] Milne-Edwards. Ann. Sc. Nat., III., 1845; Ann. Sc. Nat., VIII., 1847.

[5] Sars. Archiv f. Naturg., I., 1845.

[6] Busch. Bemerk. ueber Anat. u. Entwickel. einig. Wirbellos. Thiere, 1851; Müll. Arch., 1847.

[7] Müller. Sitzungb. Akad. Berlin, 1851, 48.

[8] Claparède. Beob. über Anat. u. Entwickel an d. Küste v. Normandie, 1863.

[9] Max Müller. Müller's Archiv, 1850, 1855.

[10] Krohn, A. Müller's Archiv, 1851; Krohn u. Schneider. Müll. Arch, 1867, Annelid larven mit porös. Hüllen.

[11] Claparède u. Metschnikoff. Zeitsch. f. Wiss. Zool, 1868.

[12] Agassiz, Alex. Young Stages of Annelids, *g*, *a*.

stomach. In our Tornaria these appendages are both of the nature of lateral plates, and are situated above the intestine. They are formed, as I have shown in a former paper on Tornaria, as diverticula of the stomach; and I have not seen, as Metschnikoff and Keferstein seem to think, the first formation of the water-system from the œsophagus. I merely took it for granted that the odd part of the water-system of Tornaria was analogous to the odd branch of the Brachiolarian water-system, and that the lateral plates corresponded to the independent branches found in Brachiolaria. The function of these lateral plates remains problematical: they do not become connected, as I formerly supposed, with the odd water-system; and their subsequent changes in the young Balanoglossus I have not been able to follow. The lateral plates are hollow at first, but eventually their walls become closely pressed together, forming lappets of considerable size, more or less banded and striated, attached along the upper edge and standing off at an angle, like parts of two inverted funnels, from the walls of the stomach, placed one within the other.

In our Tornaria the water-system is more distant from the dorsal side than in the Mediterranean species, the dorsal pore connecting with it by means of a long tube inserted on one side of the water-system: the dorsal pore also is quite eccentric, and not situated along the median dorsal line, as figured in Metschnikoff's Tornaria. The walls of the water-system are quite stout: the heart, first seen by Fritz Müller, consists of an independent vesicle, situated immediately adjoining the opening of the dorsal canal into the water-system in a sort of depression of the posterior portion of the water-system. In older stages, the heart, which can be distinctly seen to pulsate quite slowly in the earliest stages, is surrounded by an opaque membrane which does not participate in its pulsations. From the rounded posterior extremity of the water-system project two short sharp spurs riding upon the upper part of the stomach: the water-system is regularly arched laterally, slightly conical at the anterior extremity where it is connected with the anterior part of Tornaria (the base of the eye-specks) by a broad, flat, powerful muscular band which by its contraction can draw in the whole of the anterior part of Tornaria towards the mouth. I shall call anterior, dorsal, ventral, posterior, those parts of the Tornaria which correspond ultimately to the anterior, dorsal, ventral, or posterior parts of Balanoglossus.

The natural position of Tornaria in the water, while moving, is usually with the eye-specks uppermost. They revolve quite rapidly upon their longitudinal axis, and at the same time, inclining this axis, advance by a motion of translation, or revolve upon either of the extremities as a fulcrum. Previous to the transformation of Tornaria it is quite transparent: the brilliant carmine, violet, or yellow pigment-

spots are closely crowded along the broad belt of anal vibratile cilia, as well as smaller spots on the longitudinal bands of smaller cilia. The eye-specks are black and extremely prominent. The large and powerful cilia of the broad anal belt move comparatively slowly, more like the cilia of the embryos of Molluscs, as has already been observed by Müller.

Metschnikoff, in the oldest stage of Tornaria observed by him, speaks of two round bag-shaped diverticula of the œsophagus, having an internal structure similar to it, which with advancing age only increase in size. In our Tornaria the mode of formation of the pouches has been traced, and the gills (I will call them at once by their true name, from their function in the adult Balanoglossus) have been traced from their first appearance, a single pair, till there were four such pairs in the Tornaria; this is previous to any other changes. The gills are at first simply slight folds, one on each side of the dorsal part of the œsophagus: the folds gradually change into loops, then we have a series of folds, and subsequently a series of four loops, and finally, when seen from the dorsal side, the loops appear closed, forming a set of four funnels on each side, opening into the œsophagus, which from above look like round rings adjoining one another. These changes are readily followed in the figures illustrating this part of the development.

The passage of Tornaria into young Balanoglossus is very sudden, taking place in a few hours; but, unlike the transition from the Pluteus into the Echinoderm, there is no resorbition of any portion of the larva. The whole transformation consists simply in a lateral contraction of certain parts and an elongation of others, but which is sufficient, with the disappearance of the longitudinal bands of cilia, to alter completely the general aspect of the larva. The first trace of the change is the opaqueness of the larva: it loses its transparency, and somewhat its activity; the whole of the stomach is drawn down towards the intestine; the œsophagus becomes greatly elongated; and the transverse oral vibratile band is now above the junction of the stomach with the œsophagus. The œsophagus is lengthened so much that the water-system no longer rides upon the anterior part of the stomach, but is placed immediately above the opening of the mouth. The intestine has become depressed into a triangular pouch, and the stomach forms a few folds to accommodate itself to its present circumscribed space: these folds are the first trace of convolutions similar to those of the adult. During this process of lengthening of the posterior part of Tornaria, the anterior part is also greatly elongated, assuming somewhat the shape of an elliptical proboscis. In front of the circular band of cilia are plainly seen the four pairs of gills on each side of the œsophagus: this is now

divided into two portions, — one the mouth-opening of the œsophagus, the other the convoluted gill-bearing part. The pigment-cells of the longitudinal undulating bands of vibratile cilia, as well as the bands themselves, have almost disappeared. The eye-specks alone are still extremely prominent; the muscular band attached to the anterior part of the water-system has disappeared, but powerful longitudinal muscular bands as well as less marked transverse bands appear on the proboscis. The walls of the water-system have become contracted; the water-system occupies a comparatively much smaller space in the proboscis of the young Balanoglossus than in the anterior part of Tornaria. The heart can now no longer be distinguished through the opaque walls of the contracted water-system. The opening of the dorsal pore is plainly seen near the base of the proboscis.

In somewhat older stages all trace of the undulating longitudinal bands of vibratile cilia have disappeared; minute cilia, no longer arranged in bands, cover uniformly the walls of the body and proboscis. The young Balanoglossus can now be separated into three well-marked regions, — the proboscis, the collar, and the short, triangular abdominal portion. The elongation of all the parts of the Tornaria behind the proboscis is quite marked, and the distance between the collar and the anal vibratile band has become considerable. The proboscis grows more and more elongated, the body comparatively narrow and slender, while the collar-segment is better distinguished from the segment above the anal vibratile band. The part of the œsophagus from which the gills have developed lengthens more rapidly during the last stages than any other part of the young Balanoglossus. The mouth is already, as in the adult, a broad circular opening immediately under the base of the proboscis, leading into an open cavity becoming strictly an œsophagus only at the point where the gills have commenced to develop. The walls of the little worm become more and more opaque with advancing age: near the collar they generate already in the youngest stages a moderate quantity of transparent mucus, which is so abundantly and rapidly generated by the adult Balanoglossus. The few irregularly scattered pigment-cells still found upon the proboscis are the remnants of the undulating vibratile bands. In the broad anal band the cilia have lost much of their energy, vibrating but feebly and extremely slowly. The little worm no longer swims freely about, as it does in the earliest stage of its Balanoglossus existence (slightly older than the pelagic one caught by Metschnikoff), but creeps rapidly over the bottom by means of its proboscis, which acts as a sort of propeller, taking in water at the minute opening of the anterior extremity of the proboscis, and expelling it through an opening on its ventral side immediately in front of the

mouth. The eyes, during these changes, have gradually lost their prominence, becoming somewhat indistinct, and are at last completely absorbed in the walls of the proboscis in somewhat older stages. The cavity of the body is formed by two extremely thin walls extending from the base of the collar to the intestine, developed probably by the extension of the problematic bodies of the stomach, though I have never succeeded, owing to the opaqueness of the outer walls, in actually tracing this transition.

When seen from below or above, two very distinct vessels — one dorsal, the other ventral — can be traced, extending from the base of the collar to the intestine. The vessels are apparently disconnected, being pointed at the two extremities. A circular canal is formed round the œsophagus by the two forks of the water-system which saddled the upper part of the anterior portion of the stomach in Tornaria. It is connected with the heart, and opens outwards through the dorsal pore, but seems to have no connecting link as yet with the outer vessels, though in older stages this connection apparently exists.

The gills, at first circular openings leading out from the œsophagus, become gradually elliptical, then the walls nearest the middle line send out a loop, and form the first trace of the complicated folds of the gills: they do not open externally, — at least in the earlier stages raised directly from Tornaria I could not trace the opening so clearly seen in the Mediterranean species by Metschnikoff; it was only in much more advanced stages of Balanoglossus that the outward opening was discovered. Metschnikoff figures the gills as two large, funnel-shaped bodies opening on each side of a deep dorsal furrow, which is also wanting in our young Balanoglossus. I only succeeded in finding the skeleton observed by Metschnikoff as a minute granular plate in very small specimens of Balanoglossus soon after their transformation from Tornaria. The only trace of the skeleton at the base of the proboscis of Tornaria consists in an accumulation of granules similar to the granular chord lying between the chitine supports of the gills in adult specimens.

The oldest stage I succeeded in raising directly from Tornaria is a good deal older than any described by Metschnikoff, so that, unless there is an error in his observations, the formation of the gills in the European Balanoglossus must take place very slowly, as his young Balanoglossus only showed one pair of gills in the oldest stage he figures; our species commencing at once with four pairs of rudimentary gills developed almost simultaneously already during the Tornaria stage.

The smallest specimens of Balanoglossus dug up in the sand, although considerably larger than those raised directly from Tornaria, are yet sufficiently different from

the adult to leave no doubt of its identity with the Balanoglossus raised from Tornaria. The differences between them are simply differences of size and quantity. The collar is more distinct, the number of gills greater, and the convolutions of the intestine more numerous; the anal extremity has lost completely its circle of vibratile cilia. The walls of the body are scarcely more opaque than in the young Balanoglossus raised directly from Tornaria, with the exception of the proboscis, in which the muscular bands, both transverse and longitudinal, are more fully developed. The water-system and the heart could only be seen by compression; the latter, closely contracted, appeared like a solid ball at the base of the proboscis within its cavity. The anterior opening of the cavity of the proboscis is very distinct: the posterior opening is situated on the ventral side, immediately in advance of the mouth; it is quite a long, slender slit. The so-called skeleton of the proboscis is very different from that figured by Metschnikoff and Kowalevsky; it is pointed anteriorly, with two branches curving towards the ventral side, pointing towards the posterior base of the proboscis. It consists of two parts, — one apparently chitine, semi-transparent, forming the two bent forks arching towards the mouth and the other the main shaft from which the forks arise. At the head of the shaft there is a flat saucer-shaped expansion, of granular character, quite flexible, a sort of support for the base of the limber proboscis. From the base of the proboscidal skeleton there extends a granular chord as far as the extremity of the gills, to the sides of which the three branched, semi-transparent supports of the gill-folds are attached; this forms an internal skeleton in the anterior part of Balanoglossus, supporting the gill-folds, which is without parallel in the Invertebrates, unless we except some of the Ascidians. The nature and function of this skeleton is not known; the portion at the base of the proboscis may be homologized to the operculum of some of the Annelids, with which I am inclined to associate Balanoglossus. The gills are numerous, in many pairs, along the dorsal line of the anterior part, but as yet forming only slightly complicated folds, not to be compared with the complicated folds of the gills of the adult; and thus the resemblance to the young Balanoglossus raised from Tornaria is still quite complete. At the terminal extremity of the gill-system we find young gills developing from the œsophagus exactly as we have seen them develop in Tornaria.

With this preface I can now describe our common species, which differs in some very important points from the two species of Balanoglossus distinguished by Kowalevsky. I shall follow his nomenclature, and as I have nothing of any great importance to add to his exhaustive anatomy of the adult, will only compare our species with

his two, B. clavigerus, DELL. CH., and B. minutus, KOW. I shall hereafter speak of our species as Balanoglossus Kowalevskii. The New England Balanoglossus is found at low-water mark, buried in the sand (only in the cleanest sand-beaches) to a depth of about twelve or fourteen inches. It is readily tracked on the surface by the peculiar elliptical coils of sand which are thrown out at the top of the hole. The hole in which they live is lined by a thick mucous layer, forming a sort of sheath of considerable diameter, in which the worm must evidently be able to move up and down with considerable ease. Owing to the extreme tenuity of the walls of the posterior part of the body, and its great length in adult specimens, it is quite difficult to obtain complete full-grown specimens; but of the smaller sizes, where the posterior part of the body behind the gills has not yet taken a great development, it is quite easy to obtain whole specimens.

The proboscis is elongate, slightly pyriform, somewhat flattened, rounded, or pointed at the anterior extremity; it is of a pinkish-yellow color. The proboscis is attached to the upper part (dorsal) of the collar; it is rounded posteriorly, slightly indented on the median dorsal line. Seen in profile, its base of attachment is found to be quite slender; the body of the proboscis is bevelled anteriorly; the space between the lower part of the proboscis and the cavity of the collar is occupied on the base of the proboscis by the avenue leading to the mouth, a large elliptical opening capable of little expansion or contraction. The whole proboscis is occupied by a cavity opening anteriorly by a small orifice; a second opening, subsequently formed, is placed on the lower surface of the proboscis immediately in front of the mouth. The proboscis, as has already been stated by Kowalevsky, is the main organ of locomotion: water and sand are taken in at one extremity and forced out at the other, the animal moving the rest of the body by drawing it after the proboscis, which thus acts as a kind of sucker. The capacity for motion of the body situated behind the collar is limited to simply twisting and gliding, while the moving force is applied by the proboscis and collar. The proboscis is extremely variable in outline; it is capable of great expansion and contraction, the whole proboscis being lined with longitudinal and transverse muscles, which make their appearance in the earliest stages of the young Balanoglossus; the longitudinal muscles are by far the most numerous; concentric muscles are found round the two openings of the proboscis. The cavity of the proboscis has no connection whatever with the cavity of the body, into which the mouth opens, as has been correctly maintained by Kowalevsky, in opposition to the statements of Delle Chiaje and Keferstein. On the dorsal side, at the base of the proboscis, is situated the skeleton of which I have spoken above, which

probably serves as a support or fulcrum for the slender base by which the proboscis is attached to the collar. The shape of the proboscis is slightly different from that of B. minutus, being pointed anteriorly and not truncated.

Immediately behind the proboscis comes the collar, a part of the body somewhat similar to the collar of Sabella, Clymene, and allied Annelids; the anterior extremity is deeply hollowed out, the edges projecting so as to conceal the slender connecting stem of the base of the proboscis. The whole collar (as well as the proboscis, but in a less degree) is filled with glands from which an immense quantity of white transparent mucus is constantly and rapidly generated. The color of the collar is somewhat darker than that of the proboscis; it flares out both at the anterior and posterior extremity, and is slightly corrugated along the median dorsal part. The broadly open mouth leads into what corresponds to the œsophagus of Tornaria. That part of the œsophagus which is flanked by the gills is about twice as long as the proboscis, the latter being from five to six times as long as the collar.

Following the œsophagus we come to the convolutions of the former stomach, which have taken an immense development, the intestine proper remaining very much as it is in the younger stages, and occupying only a small portion of the posterior extremity of the body. The alimentary canal is connected dorsally and ventrally with the outer walls of the body along the median line, occupied by folds which are strongly ciliated and send out small branches through the windings of the alimentary canal, on each side of the large dorsal and ventral vessels, as described by Kowalevsky, the branches of the two median vessels connecting them laterally. Beyond the gills the alimentary canal is not as intimately connected with the walls as in the anterior part. The alimentary canal becomes differentiated and forms diverticula, — small, narrow folds which eventually connect with the main alimentary canal only by a narrow slit; these diverticula draw down the adjacent outer wall, forming a large number of small, elongate, narrow folds of a greenish color; these folds, lined with whitish cells, give that part of the body a most peculiar appearance. Kowalevsky calls these diverticula the liver. The limitation of the liver organs is not as well marked in the American Balanoglossus as Kowalevsky describes it in the Mediterranean species, the folds become more and more distant towards the posterior extremity, and extend far towards the anal end in the cylindrical portion of the termination of the body. Behind the liver the alimentary canal is simply formed of more or less closely packed convolutions, and it becomes almost straight near the anal extremity. In Balanoglossus Kowalevskii, immediately behind the collar, along the median dorsal line are situated the gills; they grow gradually smaller towards the pos-

terior extremity, and disappear entirely at a considerable distance behind the collar on the dorsal side. The median dorsal part of the body beyond the gills is somewhat flattened, becoming more so for the greater part of the distance occupied by the liver, the position of which is somewhat different from that which it occupies in B. clavigerus, where it extends only a short distance below the gills towards the collar; the lateral folds do not take a great development, and do not unite dorsally behind the collar, as is the case in B. minutus. The whole surface of body, as has been mentioned by previous writers on Balanoglossus, is thickly covered by minute cilia.

The gills, as I have shown from their mode of formation, consist originally of folds of the œsophagus, forming subsequently elliptical, funnel-shaped diverticula from it; from the dorsal sides of these, new folds are formed, dividing the funnels into two; and so additional folds are formed, increasing greatly the complexity of the gills, but never, in our species, forming the remarkable system of network described by Kowalevsky; nor have I been able to make out any special order in the mode of formation of the folds of the gills. Their mode of opening externally is quite different from that described by Kowalevsky. Near the dorsal median line we find a series of inverted pouches which the slightest compression will throw out like an inverted finger of a glove, forming a flat cylinder opening into a narrow slit next to the dorsal vessel, through which the gills communicate externally. The inner walls of this cylinder are strongly ciliated. The supports of the gill-folds are quite simple; the folds of the gills are supported by three prongs starting from a common curved base and attached to the more or less granular chord extending between them along the dorsal line; there is nothing to be seen of the complicated skeleton support of the gills figured by Kowalevsky for B. minutus. It is immediately on the edge of the folds that the most powerful vibratile cilia are found; owing to the increased lengthening of the central and lateral folds of the gills, they occupy a greater part of the gill-opening, and, becoming laterally crowded, appear like numerous folds placed side by side, while in reality we see only the edges of the folds, and of their skeleton supports in profile.

The genital organs occupy the same position as described by Kowalevsky for the Neapolitan species, between the liver and the anterior part of the body, forming singular bags on either side of the median line. Only a few eggs were found, and all attempts to raise them by artificial fecundation failed completely. Nor did I succeed, while digging over a large extent of ground occupied by Balanoglossus, in finding any trace of strings of eggs, as Kowalevsky suggested they might be found. The posterior part of the body is quite cylindrical, the alimentary canal having but

few convolutions. The anus terminates the short intestine as a broad opening; the edges of the walls are lined by powerful vibratile cilia. On the lower side we find on each side of the median ventral vessel a series of small folds closely packed, extending a short distance from the median line, forming a flat, corrugated band, gradually becoming narrower towards the anal extremity, extending from the collar to the posterior extremity; this band is of a light dirty-pink color, and, flanked as it is by the dark-green convolutions of the alimentary canal, is a prominent feature of the ventral side. Balanoglossus can easily be kept alive; I have kept them several weeks in confinement in jars, of which the bottom was covered with sand. The proboscis is kept continually expanding and contracting, and the sides of the body, especially of the posterior extremity, are in incessant motion.

Kowalevsky is inclined to associate Balanoglossus with the Annelids proper, and not with the Nemertians, in spite of its proboscis and its want of bristles and other appendages. This remarkable type recalls the Tunicates, from the nature of the gills and their mode of formation. It has, like Echinoderms, a ring canal; its larva is eminently echinodermoid, allied to Star-fish larvæ, which in their turn are more closely allied to the larvæ of Holothurians and Crinoids than to those of Echinoids and Ophiurans. The larva is, however, most closely allied to genuine Annelid larvæ, as Lovén's larva, though the close homology is not at first apparent, owing to the disproportion in the development of the anterior and posterior extremities in these two types. It has, like Lovén's larva, the peculiar thickening of the outer wall immediately below the two large eye-specks, as well as the muscular band leading from them. Neither of the Annelids developing from these two larvæ have any bristles, and if Schneider is correct in assigning Polygordius as the adult of Lovén's larva, we find the explanation of the two cavities lined with cilia, which he figures on each side of the anterior part of the body of Polygordius, as rudimentary gills still in the condition in which they first appear in Balanoglossus in the Tornaria stage. Both are distinctly articulated. The opening of the mouth and the structure of the alimentary canal are strikingly similar. The collar, however, is a feature which we find nowhere among Annelids except among the Sabellidae, Terebellidae, Serpulidae, Maldaniae, and the like. The presence of gills as found in Balanoglossus is a feature totally unlike that of any other group of Annelids, nor can we in any way homologize the gills with the dorsal cirri found in any group of Dorsibranchiates, as in one case they communicate directly with the œsophagus, in the other with the perivisceral cavity. In a species of Tomopteris, which is quite common on our coast, I have observed in the lateral appendages the openings first seen by Claparède, which might

be compared to the gills of Balanoglossus, but like other gill-like organs in Annelids they connect with the perivisceral cavity. Tomopteris has, however, several features which had led Claparède to regard it as intermediate between the Annelids proper and Nemertians: the absence of well-defined articulations and of setæ along the lateral appendages of the body, the setæ being limited to the cephalic appendages. We must, I think, look upon Balanoglossus as the type of a family intermediate between Tubicolous Annelids and Nemertians, to which its mode of development is closely analogous, while its structural features recall more strongly those of several families of Tubicolous Annelids. We have among Sabellidae genera in which we find a most rudimentary proboscis immediately above the opening of the mouth, on the dorsal side, under the collar; as, for instance, the genus Artacama of Malmgren.[1] Then we have such forms as Myriochile, MALM.,[2] where we find the first trace of a collar totally destitute of cephalic appendages of any sort, these taken in connection with such genera as Sabellaria, where the development of the posterior part is great, and independent, as it were, of that of the anterior part of the body, where we have a collar, gills, and dorsal cirri, as well as setæ, with all the intermediate passages afforded by the Maldaniae, Terebellidae, Sabellidae, Hermellidae, show us many features which are dimly recognized in Balanoglossus, and which link together families thus far as disconnected as the Nemertians and Tubicolous Annelids, — an association which the great similarity between the Lovén type of Annelid larva and the larvæ of Nereis and Phyllodoce shows not to be so far-fetched as might at first be imagined; hinting at a more intimate relationship between the different orders of Annelids than had thus far been recognized. It must, however, not be forgotten that the peculiar structure of the proboscis, with its openings and diverticula from the alimentary canal, are features thus far not known except among Nemertians. The lateral cephalic splits of some of the Nemertian genera correspond with the openings formed by the attachment of the proboscis, for its whole length, to the base of the collar, and their articulations are quite as distinct as in some of the Annelids. It may be that future investigations may give a different explanation of the skeleton supports of the base of the proboscis and of the gills, which would homologize them in part with the proboscidal armature of some Nemertians. Keferstein has described something analogous to the ciliated furrows of Balanoglossus in some of the Nemertians, where the lateral part of the intestine forms pouches re-entering towards the dorsal part, this being the rudimentary structure of what is so excessively developed in Balanoglossus. Van Bene-

[1] MALMGREN, A. Nordiska Hafs Annulater, Pl. XXIII. f. 60.

[2] MALMGREN, A. Annul. Polychaeta, 1867, p. 101. Pl. VII. f. 7.

den[1] has also suggested in Nemertians the existence of a rudimentary liver as diverticula from the alimentary canal. Keferstein questions the existence of two openings in the proboscis of Nemertians, as stated by Williams;[2] but from what we have found in Balanoglossus, such a structure is by no means an impossible one, even completely disconnected from the main cavity of the alimentary canal, though the explanation given by Williams of the existence of two independent stomachs is not correct; he has probably observed the water entering and leaving the proboscis, as noticed by Kowalevsky and myself in the proboscis of Balanoglossus. Kölliker[3] considers the proboscis of Nemertians as an organ of locomotion, — an opinion fully sustained by the structure and function of the proboscis of Balanoglossus. The same view is also taken by Claparède,[4] after studying the ramifications of the alimentary canal of Eurylepta.

The history of Balanoglossus as given above, while showing great analogy between the development of Echinoderms and Nemertians, by no means proves the identity of type of the Echinoderms and Annuloids. It is undoubtedly the strongest case known which could be taken to prove their identity; but when we come carefully to analyze the anatomy of true Echinoderm larvæ, and compare it with that of Tornaria, we find that we leave as wide a gulf as ever between the structure of the Echinoderms and that of the Annuloids.

[1] Van Beneden. Bull. Acad. Brux., XXXII. 1861.

[2] Williams. Report Brit. Ann., 1852.

[3] Kölliker. Schweiz. Naturforsch. Ges. 1844.

[4] Claparède, E. Recherches Anat. sur les Annel. Turbell..... d. Hébrides, 1861, p. 76.

EXPLANATION OF THE LETTERING.

a Anus.
b Branch of water-system, leading to dorsal pore.
c Collar.
d Dorsal pore.
d′ Central dorsal vessel.
d″ Flat space between *d′* and gills.
v d″ Ventral folds between *d‴* and *s*.
d‴ Central ventral vessel.
$d^{IV.}$ Flat space between *d′* and genital organs, or alimentary canal.
e Eye-specks.
f, *f′*, *f″* Folds of body-wall enclosing accumulations of mucus-secreting glands.
g Gills.
g′ Openings of gills leading outwardly.
g″ Skeleton supports of folds of gills.
g‴ Gill-folds.
$g^{IV.}$ Openings of gills leading to œsophagus.
h Heart.
i Intestine.
l Lateral flat part of the sides of the body, so-called lappets of Kowalevsky's Balanoglossus.
lv Folds of liver.
m Mouth.
m b Muscular band running from eye-speck to anterior part of the water-system.
o Œsophagus.
p Skeleton at base of proboscis in Tornaria and young Balanoglossus.
p′ Proboscis.
p″ Anterior opening of proboscis of Balanoglossus.
p‴ Posterior ventral opening of proboscis of Balanoglossus.
q Genital organs.
s Stomach or alimentary canal.
u Upper lappet of posterior extremity of stomach in Tornaria.
u′ Lower lappet of posterior extremity of stomach in Tornaria.
v Circular anal vibratile band of cilia.
v′ Longitudinal undulating bands of cilia.
w Water-system.
w′, *w′* Right and left spurs of water-system.

PLATE I.

1. Tornaria seen in profile; n. s. about $2^{mm.}$
2. Tornaria seen from ventral side; n. s. $2^{mm.}$
3. Tornaria, seen from dorsal side; n. s. about $2^{mm.}$
4. Part of the œsophagus in profile, to show the commencement of the gills as a thickening of the walls on the dorsal side, from a Tornaria somewhat younger than Fig. 1.
5. Œsophagus of Tornaria, seen in profile from mouth, *m*, to its connection with stomach, about in stage of Fig. 1.

5*a*. Œsophagus somewhat more advanced, seen from the dorsal side; commencement of two gills on each side.

6. Somewhat more advanced than Fig. 5*a*.
7. Œsophagus seen from the mouth side, about in same stages as Figs. 5 and 5*a*.
8. Œsophagus considerably more advanced, with four gills on each side, as folds of the walls of the œsophagus.
9. Œsophagus, with gills, somewhat more advanced than in Fig. 8; loops nearly closed.
10. Œsophagus seen from the mouth side, about in the same stage as in Fig. 9.
11. Œsophagus seen in profile, same state of development as preceding Figures.
12. Part of Tornaria, seen from the dorsal side, to show the relative position of the œsophagus, water-system, heart, and gills, to the digestive cavity. This is taken at about the time when Tornaria changes into Balanoglossus.
13. The water-system in profile, in a young Tornaria.
14. The same, seen from the ventral side.
15. Water-system and heart of an older Tornaria, seen in profile.
16. Water-system and heart of an old Tornaria, seen from the dorsal side.
17. Posterior extremity of the stomach of Tornaria, to show the position of the upper and lower lappets, first formed as diverticula of the stomach, seen in profile.
18. The same seen from the ventral side.

PLATE II.

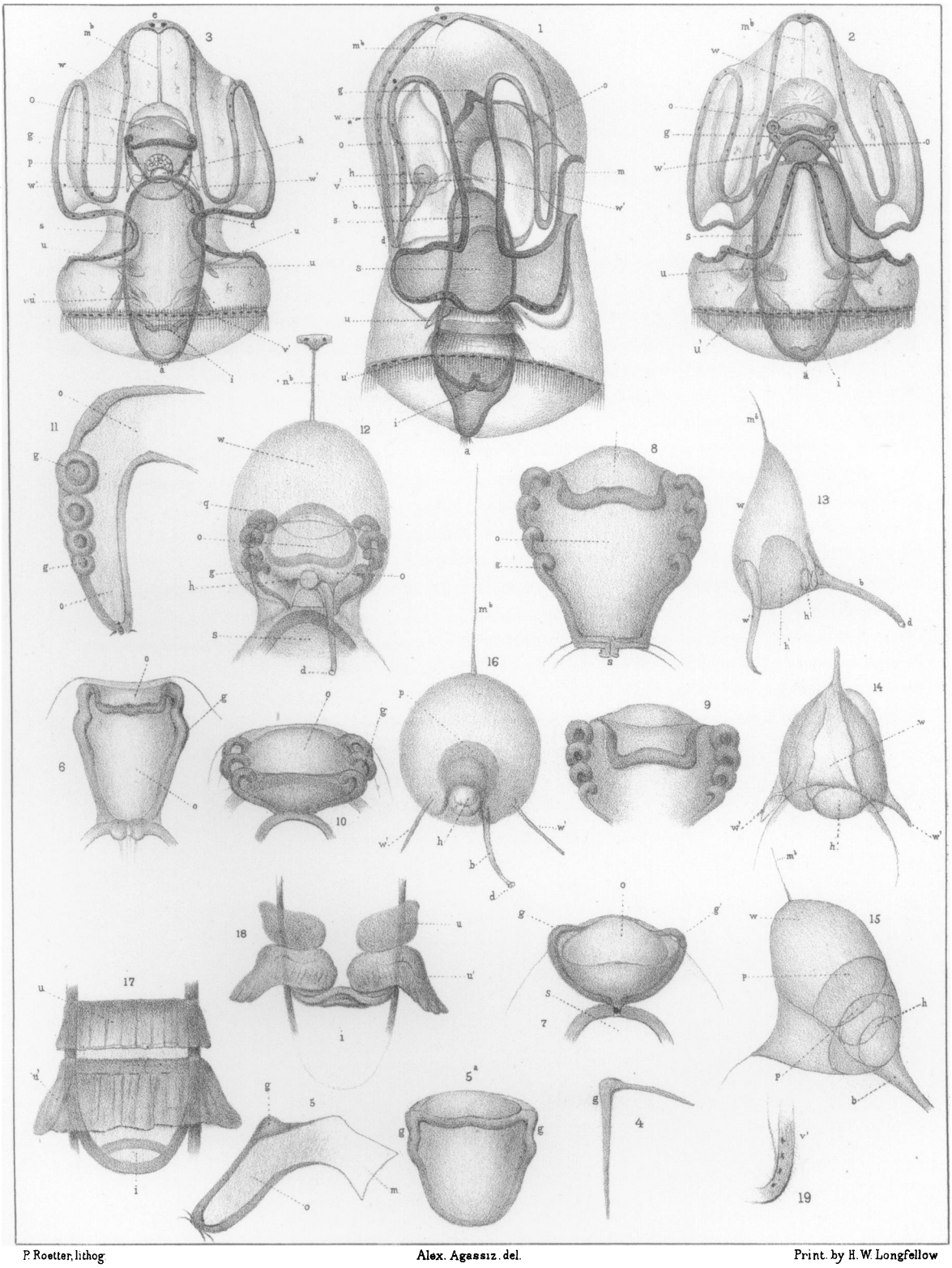
1. Tornaria, seen from the dorsal side, showing first trace of change into Balanoglossus: the posterior part of the Tornaria greatly lengthened; the longitudinal vibratile bands are reduced to indistinct lines of pigment-cells.
2. Balanoglossus in a somewhat more advanced stage, seen from the ventral side.
3. A different individual, nearly in state of Fig. 2, seen in profile.
4. Somewhat older than Fig. 3, seen from the ventral side.
5. Profile of a Balanoglossus, intermediate between Figs. 1 and 4.
6. Balanoglossus considerably older than Fig. 4, seen from the dorsal side.
7. Oldest Balanoglossus raised directly from Tornaria; body has become greatly elongated; the collar, proboscis, and posterior part of the body, are distinctly separated; the anal band of vibratile cilia is scarcely ever in movement.
8. Youngest specimen of Balanoglossus dug up from the sand, magnified two diameters, in profile.
9. The same magnified; the proboscis, collar, and gills are like those of the oldest specimens found; the genital organs and liver have as yet not been formed.
10. Anterior portion of the same somewhat more magnified.
11. Magnified portions of the convolutions of the alimentary canal, same specimen.
12. Anal portion of the same specimen, showing short intestine leading into the alimentary canal.
13. Portion of gills, to show the folds and their mode of communicating externally, from a somewhat older specimen.
14. Portion of the gills, to show mode of formation of the folds.
15. Single gill-opening, leading to œsophagus.
16. Skeleton at base of proboscis, seen from above.

16a. Same, seen in profile: the forks are curved ventrally.

17. Skeleton supporting the folds of one of the gill-openings.

PLATE III.

1. General view of a full-grown specimen of Balanoglossus Kowalevskii, as seen lying in a dish, from the dorsal side, $\frac{4}{1}$.
2. Magnified portion of the anterior part of another specimen of the same age, seen from the dorsal side.
3. Specimen very much younger, but older than the one figured on Pl. II., f. 8, seen in profile previous to the formation of the liver and of the genital organs, $35^{mm.}$ in length.
4. Magnified portion of anterior part of same (Fig. 3), seen from the ventral side.
5. Anal extremity of specimen of Fig. 1.
6. Anterior extremity of the proboscis, to show terminal opening.
7. Anterior extremity of another specimen, about the age of Fig. 3, still showing traces of the eye-specks.
8. Posterior extremity of the proboscis, to show the ventral opening contracted.
9. Posterior extremity of the proboscis of another specimen, showing the long ventral opening.
10. Portion of anal extremity of the body, seen from the ventral side.
11. Portion of ventral part of the body immediately behind the termination of the gills, covered by glands secreting mucus.
12. Portion of the dorsal part of the body a short distance behind the gills, covered by glands secreting mucus.
13. Part of the anterior portion of the sides of the body in which eggs are developed.
14. Part of the anal extremity of the body.
15. Portion of body showing the long narrow folds forming the so-called liver.



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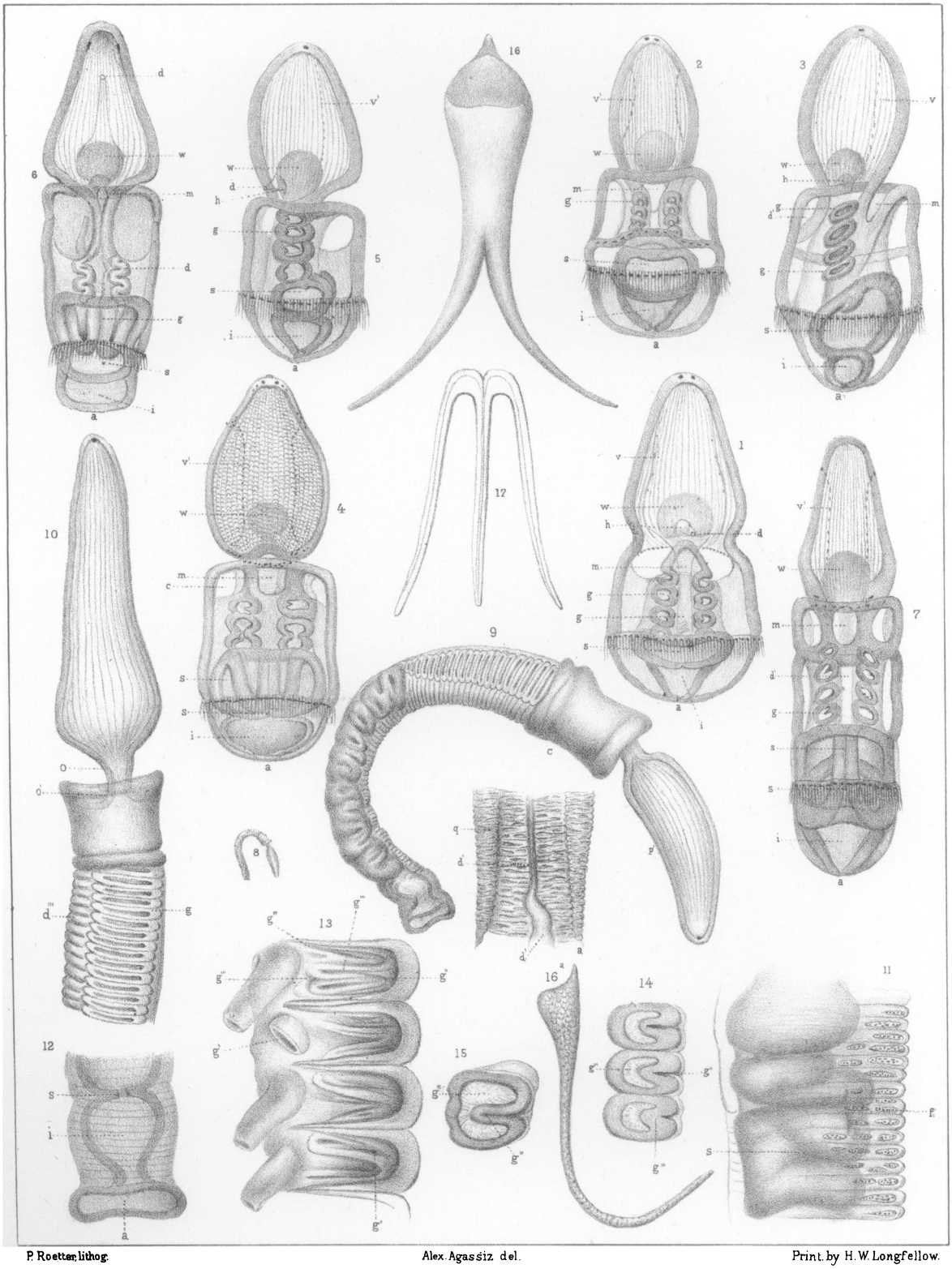

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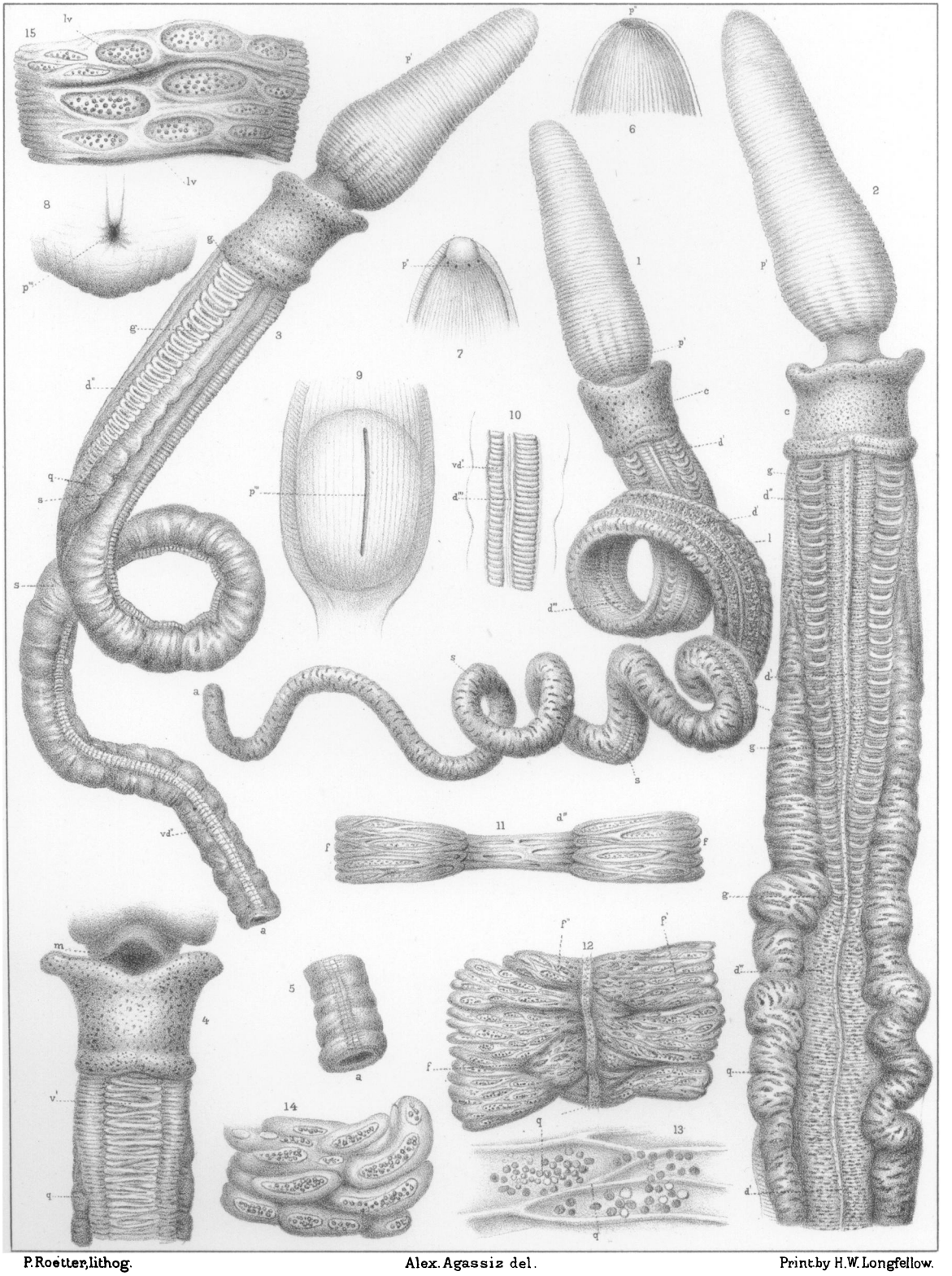

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